

## Diet of the ladybird spider *Eresus kollari* (Araneae: Eresidae) in an arid system of southeastern Spain

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**Abstract.** Spiders are a diverse and abundant group of predaceous arthropods in arid environments. Spiders in the genus *Eresus* Walckenaer, 1805 are widely distributed in mesic and arid regions of the Palaearctic, but data on their diet are scarce. The goal of this study was to analyze the diet of *Eresus kollari* Rossi, 1846 in an arid habitat of the southeastern Iberian Peninsula. A total of 64 webs of *Eresus kollari* with prey remnants were collected in a field site at the Guadix-Baza Basin, and prey were identified to species or the lowest possible taxonomic level, and counted. Prey size was estimated based on remains from the webs and voucher specimens from the study area. In addition, laboratory observations of prey capture were made. The results showed that *E. kollari* has a broad diet, including prey from a total of 106 taxa. Prey included large arthropods (mostly tenebrionids) as well as relatively small insects (e.g., ants, which constituted a high proportion of prey). Laboratory observations showed that adult *E. kollari* actively captured tenebrionid beetles crawling on silk threads around the web, and ants moving on the surface of the web sheets. The high proportion of large-size prey in the webs studied, especially tenebrionids, indicate that this spider has a diet similar to that of *Latrodectus lilianae* Melic, 2000 in the study area, but the different hunting techniques used by the two spiders probably account for the dissimilar proportion of ants and predaceous arthropods in the two diets.

**Keywords:** Prey composition, prey size, hunting technique, Coleoptera, Tenebrionidae, Formicidae

Predaceous arthropods constitute a key component of terrestrial ecosystems able to affect prey abundance and distribution (e.g., Symondson et al. 2002; Cronin et al. 2004; Woltz & Landis 2013). Spiders, a diversified and abundant group in most terrestrial ecosystems, are predatory arthropods with a relevant role in the food web of many habitats, where they are involved in an array of direct and indirect interactions, including cannibalism and intraguild predation (Wise 1993; Schmitz 1998; Denno et al. 2004). Due to the importance of spiders in food webs of arid ecosystems (Louw & Seely 1982; Polis & Yamashita 1991), studies focusing on their diet are pivotal in understanding the role of desert spiders as predators.

Spiders of the family Eresidae inhabit a variety of habitats in the Palaearctic, Afrotropical, Indomalayan, and Neotropical regions (Jocqué & Dippenaar-Schoeman 2006; Miller et al. 2012; Platnick 2013), including arid and semiarid ecosystems of the Old World (Ergashev 1979; Kuznetsov 1985; Henschel & Lubin 1992; Ward & Lubin 1993), where they may constitute abundant, albeit usually inconspicuous, predators. Several species of the genus *Eresus* Walckenaer, 1805, a Palaearctic genus with a complex taxonomy (Řezáč et al. 2008), inhabit steppe and desert ecosystems of the Palaearctic region (Ergashev 1979; Kuznetsov 1985; El-Hennawy 2004a, b). Despite being a frequent and widely distributed genus in Europe, Central Asia, North Africa, and the Middle East, studies on the biology of *Eresus*, and particularly on its diet, are very scarce (Ergashev 1979, 1983; Baumann 1997; Wisniewski & Hughes 1998; Walter 1999a, b). Although some authors have provided accounts of the prey captured by *Eresus* species, mentioning that it includes highly mobile (e.g., cicindelid beetles) and large prey (e.g., Geotrupidae and, principally, Tenebrionidae beetles) species (Berland 1932; Jones 1985; Kuznetsov 1985; Whitehead 2000), few studies have exhaustively analysed the composition of the diet of *Eresus* species (Ergashev 1979; Baumann 1997; Walter 1999a). The results of these studies, conducted in contrasting habitats,

a desert in Uzbekistan (Ergashev 1979), and pastures in Germany (Baumann 1997) and Switzerland (Walter 1999a), showed that the diet of *Eresus* spiders included large prey (mainly beetles) as well as small prey (mostly ants). However, Ergashev (1979) provided only a qualitative description of the diet, categorizing prey as rare, frequent or very abundant, while Baumann (1997) and Walter (1999a) gave quantitative data on the diet composition of *Eresus* spiders. In addition, no precise information about the hunting technique used by the spiders is available and only Ergashev (1979) provided a very general description of prey capture, indicating that after prey are caught in the web they are removed by the spider, which carries prey inside its burrow to feed on them.

In this study, we analyse the diet of *Eresus kollari* Rossi, 1846 (Fig. 1) in an arid zone of southeastern Spain. To describe the diet, we report 1) the taxonomic and size composition of the prey captured in adult female webs and 2) laboratory observations of prey capture using the two main taxa found in the webs (small ants and large tenebrionid beetles).

### METHODS

**Study area.**—The study was conducted at Barranco del Espartal (37.53° N, 2.69° W), a site in the arid Guadix-Baza Basin (southeastern Spain). The site is an occasional watercourse (*rambla*) with a gypsum loam soil. The climate is Mediterranean continental and highly seasonal, characterized by cool winters, hot summers and short springs. Rain falls mainly during the winter season (annual rainfall: 250–300 mm). Potential evapotranspiration is 3-fold the amount of precipitation. The vegetation is an open shrub-steppe (58% bare soil, 40% shrub cover) dominated by *Artemisia* (*A. herba-alba* Asso, *A. barrelieri* Besser) and *Salsola vermiculata* L. shrubs, *Macrochloa tenacissima* (L.) Kunth tussock grasses and *Retama sphaerocarpa* L. brushes. A more detailed



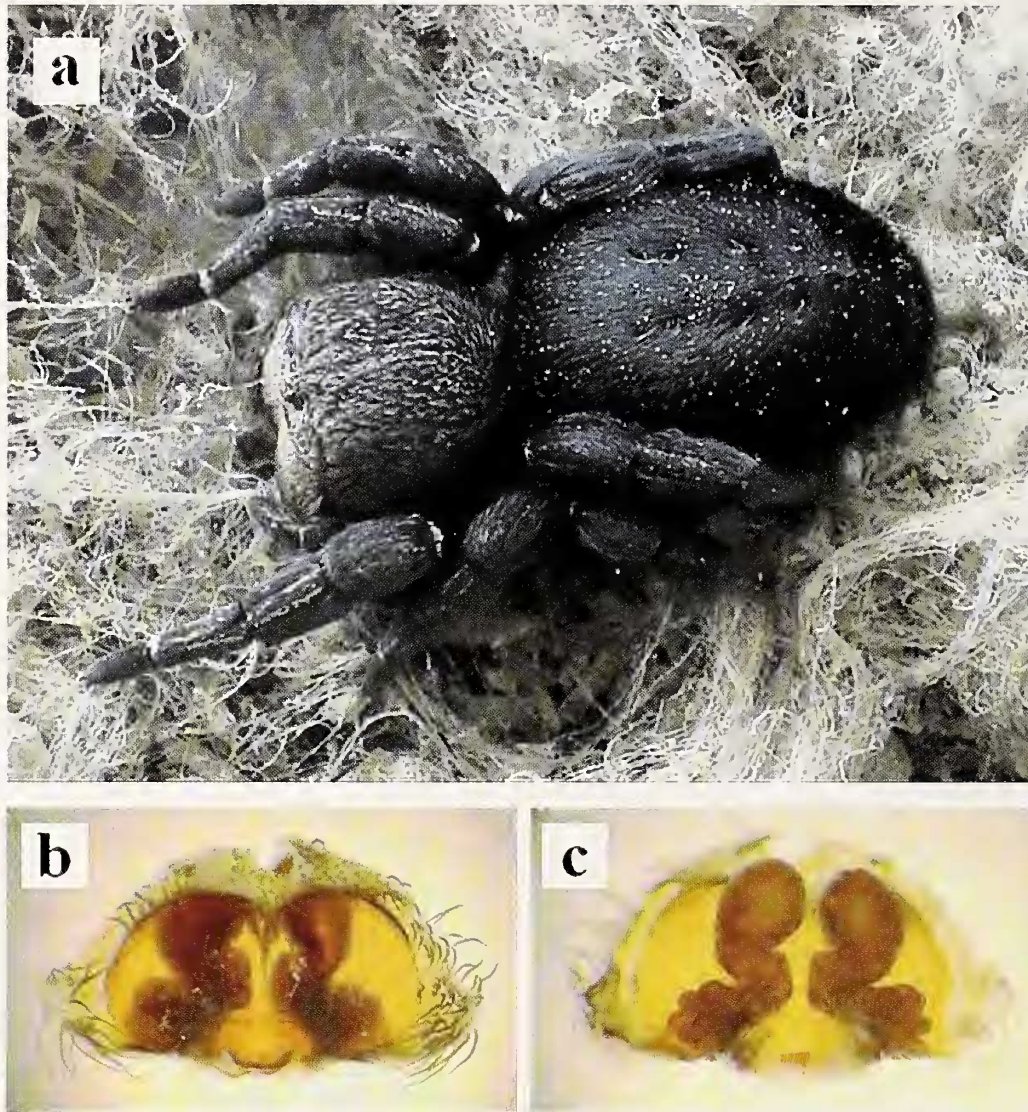


Figure 1.—Habitus (a), epigyne (b) and vulva (c) of female *Eresus kollari* from the study site. Notice that one fissure of the epigyne (the left one in this case) is deformed, a feature of the epigyne of female remains found in the nests.

description of the study site can be found elsewhere (Doblas et al. 2009).

**Natural history of *Eresus* spiders.**—*Eresus kollari* is a robust spider, prosomal length of females from central Europe ranging from 3.6 to 6.1 mm (Řezáč et al. 2008), and total body length ranging from 8.5 to 20 mm (Melic 1992; Baumann 1997). Spiders in the study area reached  $10.4 \pm 0.6$  mm (mean  $\pm$  S.E.) prosomal length and  $17.6 \pm 1.5$  mm total body length. The life cycle of the ladybird spider is completed in 3–4 years (Kuznetsov 1985; Wisniewski & Hughes 1998; Walter 1999b). After dispersal, juveniles construct simple, superficial webs and become predators (Kuznetsov 1985). Webs of older juveniles and adults have a large vertical burrow (1.5–3 cm diameter, up to 40 cm deep in our study site), sometimes including lateral branches 5–7 cm long, covered by normal silk (Jones 1985; Kuznetsov 1985; Melic 1992; Wisniewski & Hughes 1998; L. Pérez-Zarcos & F. Sánchez-Piñero, pers. obs.). The web continues with a thick mass of cribellate silk, forming a cover (Jones 1985; Kuznetsov 1985; Melic 1992; Wisniewski & Hughes 1998). The spiders keep the remains of

their prey stacked in the web (Jones 1985; Wisniewski & Hughes 1998). Since females can use the same burrow through their entire life (Jones 1985), prey contained in the webs of adult females may provide information on the prey captured by an individual over its life.

**Web collecting, prey sorting, and measurement.**—Webs of *E. kollari* were collected from November 2005 to March 2006. Because *E. kollari* webs are usually difficult to find (they are covered by sand and debris, and camouflaged with the substrate), webs were collected looking within  $50 \times 50$  cm quadrats randomly placed following transects previously established at the study site. Within each quadrat, we searched for webs using a small gardening rake. Webs were collected and placed in a container. In the laboratory, prey remains from each web were carefully separated from the silk, sorted, identified to the lowest taxonomic level possible (in large beetles and most ants to species or genus level), and counted. To analyse prey-size composition, we measured the total body length excluding appendages (rostrum, antennae, ovipositor, wings, etc.) by means of a binocular microscope equipped with



an ocular micrometer ( $\pm 0.1$  mm) or a digital calliper (in the case of large specimens). Size was measured in well-preserved prey remains or 3–10 voucher specimens per taxon from the study site kept in the collection of the Zoology Department (University of Granada, Spain).

**Laboratory observations of prey capture.**—Because previous studies (Ergashev 1983; Baumann 1997; Walter 1999a) and webs from the study site revealed that both large beetle and small ant remains were numerous in webs of adult *E. kollari*, we made laboratory observations in order to 1) determine the hunting technique used by the spider to capture prey, mainly represented by *Messor* ants and tenebrionid beetles at the study site; and 2) establish whether ants and other small prey were actual prey of adult females and not only remains from prey captured by small juveniles occurring in the webs, given that *Eresus* rarely changes burrows (see Walter 1999a). For the observations, four spiders were kept in individual terraria in the laboratory. The small number of adult spiders collected was due to the low abundance of the species in the fall 2006 and the following year, because of the large interannual variations of species abundance occurring in these arid areas (Sánchez-Piñero et al. 2011) and/or due to long life cycle in *Eresus* spiders (Walter 1999b). Each terrarium was a 25 cm length  $\times$  10 cm width  $\times$  25 cm height glass container filled with soil from the study site to a height of 18 cm and provided with a hole 10 cm deep in its centre for the spider to construct its burrow. When the spiders were placed in the containers, they occupied the burrows and built webs. For two weeks before the observations, the spiders were satiated by feeding twice a week on tenebrionid beetles (*Pimelia monticola* Rosenhauer, 1856, and *Akis discoidea* Quensel, 1806) to ensure that all the spiders had the same level of hunger.

Ant predation by adult females was observed from mid-March to late April 2008. Observations were made considering two different levels of hunger. In a first set of observations, after a week without feeding, each spider was first fed with one tenebrionid (*Pimelia monticola*) from the study site, and then three and five days later, respectively, one ant (*Messor bouvieri* Bondroit, 1918) was offered to each spider. Two rounds of this set of observations were conducted consecutively. Then, a second set of observations were conducted feeding each spider with one *P. monticola* twice per week, and then offering one ant, *M. bouvieri*, to each spider three days later. Two consecutive rounds of this set of observations were also conducted. In each observation, one ant was carefully placed in one terrarium, recording whether the ant crawled on the spider web or not, and whether the ant was captured by the spider or not after 5 min of observation (because the spiders usually did not try to capture the ant after this time). In the few cases in which the ant did not crawl on the spider web, the ant was taken out of the terrarium and the trial was not considered; then, another ant was introduced in the terrarium to start a new observation 10 min later, to avoid any potential disturbance of the spider when the observer removed the ant. If the ant crawled on the web but was not captured by the spider after the five min of observation, a second trial with a different ant was carried out about 30–60 min later. Thus, a total of 16 observations were made when spiders were fed with two tenebrionids/week and 29 trials when the spiders were fed

with one tenebrionid/week (3 in which the spider captured the first ant provided, and 13 with two consecutive trials).

## RESULTS

**Prey in the webs.**—A total of 64 webs were collected, with 2033 prey found. The webs of *E. kollari* contained prey belonging to a total of 106 taxa of 11 different Orders of arthropods, including insects (Coleoptera, Dermaptera, Dictyoptera, Hemiptera, Hymenoptera, Lepidoptera, Orthoptera), crustaceans (Isopoda), myriapods (Diplopoda) and arachnids (Solifugae, Araneae) (Appendix 1). The number of prey in the webs averaged  $31.8 \pm 2.8$  prey/web (mean  $\pm$  S.E.) ranging from zero in one web to over 100 prey in two webs (103 and 106 prey).

The diet of *E. kollari* at the study site was dominated by Coleoptera (63.11% of the prey), mostly Tenebrionidae (69.52% of the beetles), although Carabidae, Curculionidae, and Chrysomelidae were also relatively numerous in *E. kollari* webs. The other dominant prey were Formicidae (mainly *Messor bouvieri* and *M. barbarus* (Linnaeus, 1767); Appendix 1), comprising 32.96% of the prey. There was a slightly positive correlation between the number of remains of tenebrionids and ants in the webs (Pearson correlation,  $r = 0.25$ ,  $P = 0.046$ ,  $n = 64$ ). By contrast, the correlations between the number of carcasses of the remaining prey taxa as a whole and the number of remains of tenebrionids ( $r = 0.12$ ,  $P = 0.34$ ,  $n = 64$ ) and ants ( $r = 0.17$ ,  $P = 0.18$ ,  $n = 64$ ) in the webs were non-significant.

Webs of *E. kollari* showed that the diet of the spider includes a small proportion (0.64%) of predatory arthropods, most of them of relatively large size: Solifugae [*Gluvia dorsalis* (Latreille, 1817)], Araneae (Lycosidae, Gnaphosidae), predatory beetles [*Carabus linsitanicus* (Fabricius, 1801), *Cymindis lineola* Dufour, 1820, *Ocyrops ophthalmicus* (Scopoli, 1763), *Pactolinus major* (Linnaeus, 1767), *Hister grandicollis* Illiger, 1807] and assassin bugs [*Reduvius personatus* (Linnaeus, 1758)].

Prey size showed a very wide distribution, from 1.9 mm of small ants and some Curculionidae to 32.5 mm of *Blaps* tenebrionid beetles, and up to 45 mm of Julida (Fig. 2; see also Appendix 1). The prey-size distribution showed a peak occurring at 5.0–7.5 mm (corresponding to *Messor* harvester ants) and two other peaks at 12.5–15.0 mm and 17.5–22.5 mm [corresponding to the most abundant species of Tenebrionidae in the spider webs, i.e., *Sepidium bidentatum* Solier, 1844, *Pimelia baetica* Solier, 1836, *Morica hybrida* (Charpentier, 1825), and *Alphasida oberthueri* (Escalera, 1801); Appendix 1].

**Laboratory observations.**—The spiders in the terraria captured and fed on large tenebrionids as well as ants. However, the technique used for each type of prey was different. In the case of tenebrionids, the spiders captured the prey in the surroundings of the webs when the beetles walked on the peripheral strings of the web. The spiders exited the web, caught the beetles and bit them in one of the fore coxae. Large tenebrionid beetles actively fought against the spider for 30 to 60 min before the effects of the venom were noted in the prey. Then, the spiders dragged the prey into their burrows. The spiders captured ants by following the prey from under the web. Spiders would bite the web and usually it took the spiders several attempts to capture an ant. In most instances

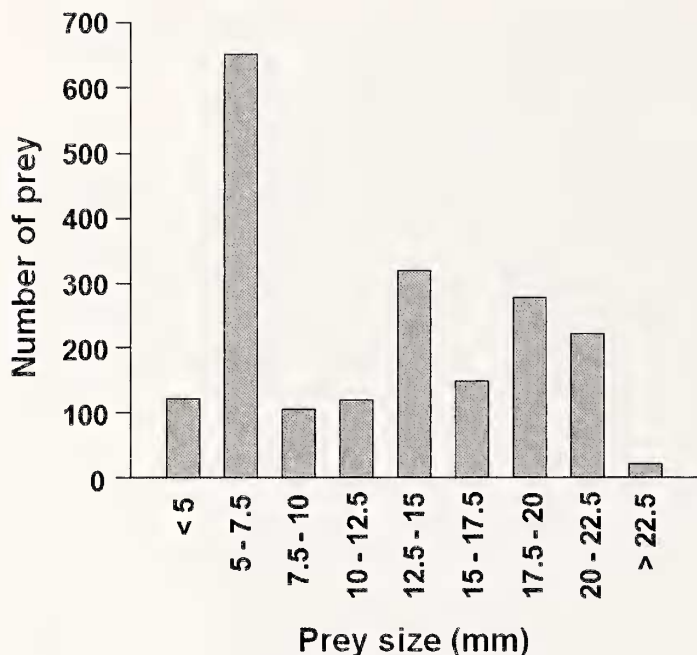


Figure 2.—Number of prey in each size category found in the webs of *E. kollari*.

(21 out of 29 trials in which the spider attempted to capture the ant, i.e., about 3/4 of the attempts), the spiders were unable to catch the ants.

The capture of prey, especially ants, depended on hunger level of the spiders, as spiders did not respond to prey (large or small) if they had previously been satiated. Also, when regularly fed with tenebrionids (twice a week), spiders did not respond to ants and only attempted to capture ants when tenebrionids were offered less frequently (once a week). In this case, only about 1/4 of the ants (8 out of 29 ant trials) were captured by the spider.

## DISCUSSION

*Eresus kollari* from arid zones of the Guadix-Baza Basin kept in the laboratory actively captured prey crawling on silk threads around the web (in the case of tenebrionids) or tried to capture prey moving on the web sheet by biting along the web sheet from below (in the case of ants). For large tenebrionids, it was surprising to observe the fierce fighting of the spider with the beetle for a relatively long time before the predator was able to drag the almost paralyzed prey inside the web. These observations contrast with the hunting technique of capturing prey caught in the web reported by Ergashev (1979). Whether the two hunting techniques observed are used to capture small and large prey in general and whether entanglement in the web constitutes a further mechanism to capture other prey types remain open questions.

Our results reveal that *E. kollari* in arid zones of the Guadix-Baza Basin feeds on a wide range of prey, from large arthropods, such as most tenebrionids, to small insects, such as ants. The diet was amply dominated by Tenebrionidae and Formicidae, which comprised more than 75% of the number of remains found in the spider webs. The fact that these prey had a relatively thick cuticle and their remains were well

preserved in the webs may lead to an overestimation of these taxa in the diet of *E. kollari*. However, the potential degradation of prey remains in the webs did not appear to constitute an important bias in our results. Firstly, only remains exposed on the surface of the webs showed some decoloration by sun bleaching, but all these remains were unequivocally identifiable. Secondly, soft-bodied insect larvae and invertebrates in arid systems are primarily belowground dwellers to avoid desiccation and exposure to extreme temperatures (Wallwork 1982), and thus are not preyed upon by *E. kollari*. In addition, most soft-bodied insect larvae in the study area (mainly Coleoptera and Lepidoptera; Sánchez-Piñero 1994; Doblas et al. 2007) were easily identified in the webs by the well-preserved sclerotized cephalic capsules, although in most cases there were also remains of the body cuticle (making it possible even to identify tenebrionid larvae to the genus level). Furthermore, on the soil surface and in the litter, the very low abundance of lightly sclerotized Diptera larvae lacking a cephalic capsule (< 1% in litter; Doblas et al. 2007), and the absence in superficial soil levels of the scarce *Allolobophora caliginosa* (Savigny, 1826) earthworms (Doblas et al. 2007) makes the potential bias provoked by the degradation of their remains likely unimportant. Finally, most larvae are not very vagile animals, reducing their probability of being preyed upon by *E. kollari*. Thus, the proportion of larvae collected in pitfall traps in the study area (0.5–0.9%; Sánchez-Piñero 1994) was similar to the proportion of larvae found in *E. kollari* webs (0.54%). Nonetheless, an experimental assessment of the degradation of prey remains in the webs would enhance the accuracy of diet information gathered from studying the spider webs.

Although our results cannot be easily compared to the data provided by previous studies (Ergashev 1979; Baumann 1997; Walter 1999a), there are some remarkable similarities in the diet of *Eresus* spiders. On one hand, the most abundant remains in the webs were beetles and ants. Ants occurred not only in similar proportions in the webs of the spider both in Switzerland (36.6%) and southeastern Iberian Peninsula (33%), but were also very abundant items in Uzbekistan, although they constituted only some 10% of the remains found in the webs in Germany. Tenebrionid beetles constituted the main prey in the present study and were also reported as very abundant prey in the central Asian desert by Ergashev (1979), although this author did not specify whether these beetles were the most abundant prey in the spider webs. However, in central Europe the most abundant beetle prey were Carabidae (21% to >40% of prey), a group found in a much lower proportion in the diet of *Eresus* in arid areas of Spain (5.5% of the total number of prey) and Uzbekistan (recorded as frequent prey). On the other hand, there were some differences, as the high abundance of orthopterans and sphecid wasps in the spider webs analyzed by Ergashev (1979), and the frequent occurrence of honey bees both in Uzbekistan and Switzerland. These differences can be explained by the contrasting prey availability among sites, as suggested by the generalist diet of *E. kollari*.

The high proportion of Tenebrionidae and Formicidae in the webs of *E. kollari* in the Baza Basin would be related to the fact that these are the dominant groups in the study area (Sánchez-Piñero 1994; Sánchez-Piñero et al. 2011), indicating



the generalist character of *E. kollari* diet. This is also corroborated by the fact that the most abundant remains in the webs (the tenebrionids *Pimelia baetica*, *Sepidium bidentatum*, *Alphasida obertlneri*, and *Morica hybrida*, and the ants *Messor bouvieri* and *M. barbarus*) coincide with the most abundant taxa in the study area (Sánchez-Piñero 1994; Sánchez-Piñero et al. 2011). The slightly positive correlation between the number of remains of tenebrionids and ants in the webs is presumably related to the fact that tenebrionid beetles in the study area aggregate in ant-nest mounds (Sánchez-Piñero & Gómez 1995). Nevertheless, the percentage of tenebrionids preyed upon by the spider (43.62%) is much higher than the percentage of these beetles captured in pitfall traps reported in previous studies at the study site (3.3–16.9% of all arthropods captured; Sánchez-Piñero et al. 2011). By contrast, ants, the numerically dominant taxa at the study site, appeared in the webs of *E. kollari* in a lower proportion (33.7%) than in the pitfall-trap data (49.1–57.1% of the total number of arthropods collected; Sánchez-Piñero et al. 2011). Although these data could be interpreted as a preference of *E. kollari* for large prey, our observations suggest that the lower proportion of ants in the webs in comparison to their abundance at the study site is also probably related to the limited success of the spiders in capturing ants crawling on the web sheets, although the proportion of ants captured by spiders in the laboratory may differ from the proportion captured under natural conditions.

Besides the preference and/or higher capture success of *E. kollari* for large prey, ants (mainly *Messor bouvieri* and *M. barbarus*) still constitute a dominant item in the diet of this spider in the study area. Ants could be so abundant in webs because: 1) they were preyed upon only when the spiders were small juveniles, and remains occurred in the webs because *Eresus* rarely changed their burrows; or 2) ants are actually preyed by adult females (see Walter 1999a). Our laboratory observations showed that adult *E. kollari* actually captured and fed on ants, although they preferred large prey. Surprisingly, five webs of spiders of 5–6 mm in body length (difficult to find, because the small, flat webs were usually concealed in minor cracks or depressions in the soil) collected showed a high proportion of large tenebrionids (31 individuals, 32% of prey) and ants (33 individuals, 34% of prey), indicating that both small and large *E. kollari* were able to capture prey in a similar size range. A plausible explanation for the high number of ants in *E. kollari* webs is that ants are not only the numerically dominant taxon at the study site, but also they remain active year round in the area and may constitute the staple food for the spider in winter and early spring, when tenebrionid beetles are practically inactive and ants and small insects are the main prey available (Sánchez-Piñero 1994; L. Pérez-Zarcos & F. Sánchez-Piñero pers. obs.). The importance of ants in the diet of ground spiders during the winter has been indicated for large trap-door spiders (Buchli 1969; Bradley 1996; Decay et al. 2007; Pérez-Zarcos, pers. obs.). Ants are also important food items during the winter in the study area for sedentary birds, such as *Oenanthe leucura* (Gmelin, 1789) (Muscicapidae) and *Galerida theklae* (Brehm, 1858) (Alaudidae) (Hódar 1993, 1995). Thus, ants may be important prey for the long-lived *E. kollari*, which have to survive for several winters in a habitat where ants are

among the few arthropods able to forage during the cold months.

The high proportion of large arthropods (especially tenebrionids), the presence of predatory arthropods in webs, and the potential predation of *Eresus* spiders on lizards, as recorded in the desert systems of Uzbekistan (Ergashev 1979), reveal that this species has a diet similar to that of the black widow spider *Latrodectus lilianae* Melic, 2000 in the Guadix-Baza Basin (Hódar & Sánchez-Piñero 2002). The similarity of the diet of both spiders is also corroborated by the fact that the same tenebrionid species (*Pimelia* spp., *Sepidium bidentatum* and *Alphasida obertlneri* – recorded as *A. clementei* in Hódar & Sánchez-Piñero 2002) were the main prey items in the webs of both *L. lilianae* and *E. kollari* (Hódar & Sánchez-Piñero 2002). However, there are two important differences between the diets of these two spiders. First, although the diet of *E. kollari* at the study site included large predatory arthropods, intraguild predation appears less relevant in the diet of *E. kollari* (0.6%) than in the black widow (4–14%; Hódar & Sánchez Piñero 2002) in the study area. Second, there was a lower proportion of ants in the diet of *L. lilianae* (0.2–8.7% of the prey). The difference in the relative proportions of ants in the diets of these two spiders can be explained by the fact that prey captured by *L. lilianae* are constrained by the size of the prey able to break the strings of the web (Hódar & Sánchez-Piñero 2002), while *E. kollari* appears to be limited only by the ability of the spider to capture the prey while moving on the web surface.

In conclusion, the diet of *E. kollari* showed a wide variety of prey both taxonomically and in terms of prey size, and it is dominated by large tenebrionid beetles and formicids, the two dominant taxa in the study area. The potential role of ants as an important resource for winter survival in these spiders is a question requiring further investigation.

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#### LITERATURE CITED

- Baumann, T. 1997. Populationsökologische und zönotische Untersuchungen zur Bedeutung von Habitatqualität und Habitatfragmentierung für Spinnenpopulationen auf Trockenrasen am Beispiel von *Eresus cimaberinus* (Oliv. 1789). Wissenschaft und Technik Verlag, Berlin.
- Berland, L. 1932. Les Arachnides. Paul Lechevalier et fils, Paris.
- Bradley, R.A. 1996. Foraging activity and burrow distribution in the Sydney brown trapdoor spider (*Misgolas rapax* Karsch: Idiopiidae). *Journal of Arachnology* 24:58–67.

- Buchli, H.H.R. 1969. Hunting behavior in the Ctenizidae. *American Zoologist* 9:175–193.
- Cronin, J.T., K.J. Haynes & F. Dilleuth. 2004. Spider effects on planthopper mortality, dispersal, and spatial population dynamics. *Ecology* 85:2134–2143.
- Decay, A., P. Cardoso & P. Selden. 2007. Taxonomic review of the Portuguese Nemesiidae (Araneae, Mygalomorphae). *Revista Ibérica de Aracnología* 14:1–18.
- Denno, R.F., M.S. Mitter, G.A. Langellotto, C. Gratton & D.L. Finke. 2004. Interactions between a hunting spider and a web builder: Consequences of intraguild predation and cannibalism for prey suppression. *Ecological Entomology* 29:566–577.
- Doblas, E., F. Sánchez-Piñero & A. González-Megías. 2007. Soil macroinvertebrate fauna of a Mediterranean arid system: Composition and temporal changes in the assemblage. *Soil Biology and Biochemistry* 39:1916–1925.
- Doblas, E., F. Sánchez-Piñero & A. González-Megías. 2009. Different structuring factors but connected dynamics shape litter and belowground macrofaunal food webs. *Soil Biology and Biochemistry* 41:2543–2550.
- El-Hennawy, H.K. 2004a. Review of spiders of genus *Eresus* in Egypt (Araneida: Eresidae). *Serket* 9:25–35.
- El-Hennawy, H.K. 2004b. A new species of genus *Eresus* from Algeria (Araneida: Eresidae). *Serket* 9:1–4.
- Ergashev, N.E. 1979. The trophic relations of the spider *Eresus niger* Pet. *Uzbekskii Biologicheskii Zhurnal* 5:60–62.
- Ergashev, N.E. 1983. An interesting phenomenon in the reproduction of spiders *Eresus niger* Pet., *Stegodiphus lineatus* Latr. (family Eresidae). *Doklady Akademii Nauk Uzbekskoi SSR* 10:51–52.
- Henschel, J.R. & Y.D. Lubin. 1992. Environmental factors affecting the web and activity of a psammophilous spider in the Namib Desert. *Journal of Arid Environments* 22:173–189.
- Hódar, J.A. 1993. Relaciones tróficas entre los Passeriformes insectívoros en dos zonas semiáridas del sureste peninsular. PhD Thesis. Universidad de Granada, Granada.
- Hódar, J.A. 1995. Diet of the black wheatear *Oenanthe leucura* in two shrubsteppe zones of southeastern Spain. *Alauda* 63:229–235.
- Hódar, J.A. & F. Sánchez-Piñero. 2002. Feeding habits of the blackwidow spider *Latrodectus lilianae* (Araneae: Theridiidae) in an arid zone of south-east Spain. *Journal of Zoology* 257:101–109.
- Jocqué, R. & A.S. Dippenaar-Sehoeman. 2006. Spider Families of the World. Royal Museum for Central Africa, Tervuren, Belgium.
- Jones, D. 1985. Guía de campo de los arácnidos de España y Europa. Omega, Barcelona.
- Kuznetsov, G.T. 1985. [On the ecology of spiders *Eresus niger* Pet. and *Lithyphantes paykullionus* Walck. (Aranei, Eresidae, Theridiidae) in south Turkmenistan.] *Izvestiya Akademii Nauk Turkmenskoi SSR Seriya Biologicheskikh Nauk* 1985 (6):70–72 (in Russian).
- Louw, G. & M. Seely. 1982. *Ecology of Desert Organisms*. Longman, London.
- Melic, A. 1992. La familia Eresidae (Arachnida: Araneae) en Aragón. *Notas aracnológicas aragonesas*, 4. *Boletín de la Sociedad Entomológica Aragonesa* 11:7–12.
- Miller, J.A., C.E. Griswold, N. Scharff, M. Řezáč, T. Szűts & M. Marhabaie. 2012. The velvet spiders: an atlas of the Eresidae (Arachnida, Araneae). *ZooKeys* 195:1–144.
- Platnick, N. I. 2013. The world spider catalog, version 14.0. American Museum of Natural History, online at <http://research.amnh.org/iz/spiders/catalog/>
- Polis G.A. & T. Yamashita. 1991. The ecology and importance of predaceous arthropods in desert communities. Pp. 180–222. *In* *The Ecology of Desert Communities*. (G.A. Polis, ed.). University of Arizona Press, Tucson, Arizona.
- Řezáč, M., S. Pekár & J. Johannesen. 2008. Taxonomic review and phylogenetic analysis of central European *Eresus* species (Araneae: Eresidae). *Zoologica Scripta* 37:263–287.
- Sánchez-Piñero, F. 1994. *Ecología de las comunidades de coleópteros en zonas áridas de la Depresión de Guadix-Baza (sureste de la Península Ibérica)*. Ph.D Thesis, University of Granada.
- Sánchez-Piñero, F. & J.M. Gómez. 1995. Use of ant-nest debris by darkling beetles and other arthropod species in an arid system in South Europe. *Journal of Arid Environments* 31:91–104.
- Sánchez-Piñero, F., A. Tinaut, A. Aguirre-Segura, J. Miñano, J.L. Lencina, F.J. Ortiz-Sánchez et al. 2011. Terrestrial arthropod fauna of arid areas of SE Spain: Diversity, biogeography, and conservation. *Journal of Arid Environments* 75:1321–1332.
- Schmitz, O.J. 1998. Direct and indirect effects of predation and predation risk in old-field interaction webs. *American Naturalist* 151:327–342.
- Symondson, W.O.C., K.D. Sunderland & M.H. Greenstone. 2002. Can generalist predators be effective biocontrol agents? *Annual Review of Entomology* 47:561–594.
- Wallwork, J.A. 1982. *Desert Soil Fauna*. Praeger, New York.
- Walter, J.E. 1999a. Durer's rhinoceros and the prey of *Eresus cimaberinus* (Olivier) (Araneae: Eresidae). *Arachnologische Mitteilungen* 17:11–19.
- Walter, J.E. 1999b. Lebenszyklus von *Eresus cimaberinus* (Olivier, 1789) (Araneae: Eresidae) in der Schweiz. *Mitteilungen der Entomologischen Gesellschaft Basel* 49:2–7.
- Ward, D. & Y. Lubin. 1993. Habitat selection and the life history of a desert spider, *Stegodyphus lineatus* (Eresidae). *Journal of Animal Ecology* 62:353–363.
- Whitehead, P.F. 2000. Coleoptera in the diet of *Eresus walckenaeri* Brulle (Araneae, Eresidae) in Zakynthos, Ionian Islands, Greece. *Entomologist's Monthly Magazine* 136:205–206.
- Wise, D.H. 1993. *Spiders in Ecological Webs*. Cambridge University Press, Cambridge.
- Wisniewski, P.J. & I. Hughes 1998. The ladybird spider *Eresus cimaberinus* rearing project. *International Zoo Yearbook* 36:158–162.
- Woltz, M. & D.A. Landis. 2013. Coccinellid immigration to infested host patches influences suppression of *Aphis glycines* in soybean. *Biological Control* 64:330–337.

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Appendix 1.—Prey taxa, number of individuals for each taxon, and prey size (mean  $\pm$  S.E.) collected from webs of *E. kollari*.

Taxa	Number of prey	Prey size (mm)
<b>CHELICERIFORMES</b>		
<b>Solifugae</b>		
Daesiidae		
<i>Ghivva dorsalis</i> (Latreille, 1817)	1	20.0
<b>Araneae</b>		
Lycosidae	1	15.0
Gnaphosidae	1	10.0
<b>CRUSTACEA</b>		
<b>Isopoda</b>		
Oniscidae	4	16.5
<b>HEXAPODA</b>		
<b>Blattodea</b>		
Blattellidae		
<i>Ectobius</i> sp.	3	7.5 $\pm$ 0.6
<b>Coleoptera</b>		
Anthicidae		
<i>Notoxus</i> sp.	2	4.5 $\pm$ 0.1
Buprestidae		
<i>Inlodus onopordi</i> (Fabricius, 1787)	7	25.1 $\pm$ 1.1
<i>Acuataederella moroderi</i> (Reitter, 1906)	1	7.1
Carabidae		
<i>Acinopus picipes</i> (Olivier, 1795)	10	13.5 $\pm$ 0.5
<i>Carabus lusitanicus</i> (Fabricius, 1801)	3	24.3 $\pm$ 0.8
<i>Cymindis lineola</i> Dufour, 1820	1	11
<i>Dixus capito</i> (Serville, 1821)	46	13.5 $\pm$ 0.3
<i>Dixus sphaerocephalus</i> (Olivier, 1795)	25	8.7 $\pm$ 0.1
<i>Eriotomus villosulus</i> (Reiche, 1859)	1	6.9
<i>Harpalus tenebrosus</i> Dejean, 1829	1	9.7
<i>Orthomus barbarus</i> Dejean, 1828	21	9.85 $\pm$ 0.2
<i>Poecilus cupreus</i> (Linnaeus, 1758)	1	13.5
Carabidae larvae	4	-
Unidentified Carabidae	2	-
Cerambycidae		
<i>Iberodorcadion mnicidum</i> (Dalman, 1817)	5	22.4 $\pm$ 0.9
Chrysomelidae		
<i>Chrysolina bankii</i> (Fabricius, 1775)	3	10.4 $\pm$ 0.2
<i>Chrysolina affinis</i> (Fabricius, 1787)	2	8.1 $\pm$ 0.1
<i>Chrysolina diluta</i> (Germar, 1824)	13	7.0 $\pm$ 0.2
<i>Chrysolina jan-bechynei</i> Cobos, 1953	4	8.1 $\pm$ 0.5
<i>Coptocephala scopulina</i> (Linnaeus, 1767)	1	7.3
<i>Cyrtous plumbeus</i> Fairmaire, 1850	7	8.1 $\pm$ 0.9
<i>Galernca angusta</i> (Küster, 1849)	46	10.4 $\pm$ 0.1
Unidentified Chrysomelidae	2	-
Curculionidae		
<i>Aspidiotes westringii</i> Schoenherr, 1847	10	7.0 $\pm$ 0.2
<i>Brachycerns pradieri</i> Fairmaire, 1856	8	9.3 $\pm$ 1.8
<i>Coniocleonus tabidus</i> (Olivier, 1790)	36	11.7 $\pm$ 0.8
<i>Cycloderes glabratus</i> (Gyllenhal, 1833)	14	8.0 $\pm$ 0.1
<i>Larinus flavescens</i> Germar, 1824	1	15.45
<i>Ocladus gaudii</i> Osella & Meregalli, 1987	1	5.3
Rhytirhinini	4	5.1 $\pm$ 0.6
<i>Sibinia iberica</i> Hoffmann, 1959	3	2.2 $\pm$ 0.2
Trachyphloenini	2	3.5 $\pm$ 0.5
<i>Xanthochelus cinctiventris</i> (Fahaeus, 1842)	1	16.0
Unidentified Curculionidae	24	4.1 $\pm$ 1.7
Elateridae		
<i>Cebrio</i> spp.	1	14.1 $\pm$ 0.6
<i>Cardiophorus</i> sp.	6	7.0 $\pm$ 0.2
<i>Melanothrus</i> sp.	4	12.7 $\pm$ 0.6

Appendix 1.—Continued.

Taxa	Number of prey	Prey size (mm)
<b>Histeridae</b>		
<i>Hister grandicollis</i> Illiger, 1807	1	10.5
<i>Pactolinus major</i> (Linnaeus, 1767)	1	13.0
<b>Melyridae</b>		
<i>Graellsinus praticola</i> (Waltl, 1835)	3	5.4 $\pm$ 0.2
Malachiinae	2	4.6 $\pm$ 0.1
Unidentified Melyridae	1	4.8 $\pm$ 0.2
<b>Scarabaeidae</b>		
<i>Aphodius baeticus</i> (Mulsant & Rey, 1869)	17	6.8 $\pm$ 0.2
<i>Bolbelasmus bocchus</i> (Erichson, 1841)	3	14.0 $\pm$ 0.5
<i>Rhizotrogus toletanus</i> Báguena, 1955	15	11.5 $\pm$ 0.5
<b>Staphylinidae</b>		
<i>Ocyopus ophthalmicus</i> (Scopoli, 1763)	3	26.5 $\pm$ 1.2
<b>Tenebrionidae</b>		
<i>Akis discoidea</i> Quensel, 1806	2	22.0 $\pm$ 2.0
<i>Alphasida oberthueri</i> (Escalera, 1901)	124	20.0 $\pm$ 0.5
<i>Alphasida rectipennis</i> (Escalera, 1906)	26	18.8 $\pm$ 0.5
<i>Alphasida</i> sp. larvae	1	-
<i>Asida oblonga frigida</i> Escalera, 1905	55	13.4 $\pm$ 0.5
<i>Asida</i> sp.	1	12.8
<i>Blaps lusitanica</i> Herbst, 1799	2	28.8 $\pm$ 0.5
<i>Blaps nitens brachyura</i> Küster, 1848	2	27.0 $\pm$ 0.5
<i>Blaps waltli</i> Seidlitz, 1893	1	32.5
<i>Crypticus antoinei</i> Español, 1950	2	7.1 $\pm$ 0.2
<i>Leptoderis collaris</i> (Linnaeus, 1767)	1	20.0
<i>Morica hybrida</i> (Charpentier, 1825)	87	20.2 $\pm$ 0.5
<i>Phylau gibbnus</i> (Motschoulsky, 1849)	2	9.1 $\pm$ 0.1
<i>Pimelia baetica</i> Solier, 1836	251	17.9 $\pm$ 0.4
<i>Pimelia monticola</i> Rosenhauer, 1856	66	16.6 $\pm$ 0.3
<i>Pimelia</i> sp. larvae	1	-
<i>Probaticus interstitialis</i> (Küster, 1850)	7	13.4 $\pm$ 0.9
<i>Scaurus rugulosus</i> Solier, 1838	5	15.6 $\pm$ 1.4
<i>Scaurus micinus</i> (Forster, 1771)	65	15.7 $\pm$ 0.8
<i>Sepidium bidentatum</i> Solier, 1844	164	14.1 $\pm$ 0.4
<i>Tentyria laevis</i> Solier, 1835	27	14.3 $\pm$ 2.3
Unidentified Coleoptera	22	-
<b>Dermaptera</b>		
<b>Forficulidae</b>		
<i>Forficula amricularia</i> Linnaeus, 1758	3	17.0 $\pm$ 2.0
<b>Hemiptera</b>		
<b>Cercopidae</b>		
<i>Cercopis</i> sp.	1	10.3 $\pm$ 0.8
Dyctiopharidae	2	3.6 $\pm$ 0.1
<b>Cydnidae</b>		
<i>Aethus pilosus</i> (Herrich-Schaeffer, 1834)	1	6.5
<i>Legnotus fumigatus</i> (A. Costa, 1853)	1	4.0
<i>Tritomegas</i> cf. <i>theryi</i> (Lindberg, 1932)	1	6.3
<b>Lygaeidae</b>		
<i>Plinthinus</i> cf. <i>lepineyi</i> Vidal, 1940	1	4.2
<b>Pentatomidae</b>		
<i>Aelia</i> sp.	2	15.0 $\pm$ 0.3
<i>Aelia cribrata</i> Fieber, 1868	10	9.9 $\pm$ 1.0
<i>Ancyrosoma lencogrammus</i> (Gmelin, 1790)	1	6.5
<i>Carpocoris</i> cf. <i>fuscipennis</i> (Boheman, 1849)	1	10.1
<i>Irochrotus maculiventris</i> (Germar, 1839)	2	8.8
Unidentified Pentatomidae	1	-
<b>Pyrrocoridae</b>		
<i>Codophila varia</i> (Fabricius, 1787)	1	11.1
<i>Pyrrocoris apterus</i> (Linnaeus, 1758)	1	11.0

## Appendix I.—Continued.

Taxa	Number of prey	Prey size (mm)
Reduviidae		
<i>Reduvius personatus</i> (Linnaeus, 1758)	1	10.0
Scutelleridae		
<i>Psacasta</i> sp.	1	8.8
Stenocephalidae		
<i>Dicranocephalus</i> sp.	1	14.0
<b>Hymenoptera</b>		
Formicidae		
<i>Aphaenogaster ibérica</i> Emery, 1908	14	6.5 ± 0.7
<i>Camponotus</i> sp.	23	6.0 ± 2.8
<i>Cataglyphis ibérica</i> Emery, 1906	18	5.5 ± 2.1
<i>Crematogaster</i> sp.	23	3.5 ± 0.7
<i>Gonionna</i> sp.	3	3.9 ± 0.6
<i>Messor</i> spp.	529	5.6 ± 0.9
<i>Pheidole pallidula</i> (Nylander, 1848)	1	2.1
<i>Proformica</i> sp.	2	6.0 ± 2.8
<i>Tapinoma</i> sp.	44	1.9 ± 0.5
<i>Tetramorium</i> spp.	13	3.5 ± 0.7
Sphecidae	1	14.5
Bethylidae	2	9.9 ± 1.0
Unidentified Hymenoptera	26	-
<b>Lepidoptera</b> (larvae)	6	-
<b>Orthoptera</b>		
Acrididae		
<i>Mioscirtus wagneri</i> (Kittary, 1859)	1	15.6 ± 0.2
MYRIAPODA		
<b>Julida</b>		
Julidae	2	33.3 ± 1.8